

24. Shen, Y., Knoll, A. H. & Walter, M. R. Evidence for low sulphate and anoxia in a mid-Proterozoic marine basin. *Nature* **423**, 632–635 (2003).
25. Shen, Y., Canfield, D. E. & Knoll, A. H. Middle Proterozoic ocean chemistry: Evidence from the McArthur Basin, northern Australia. *Am. J. Sci.* **302**, 81–109 (2002).
26. Brennan, S. T., Lowenstein, T. K. & Horita, J. Seawater chemistry and the advent of biocalcification. *Geology* **32**, 473–476 (2004).
27. Knoll, A. H., Hayes, J. M., Kaufman, A. J., Swett, K. & Lambert, I. B. Secular variation in carbon isotope ratios from Upper Proterozoic successions of Svalbard and East Greenland. *Nature* **321**, 832–838 (1986).
28. Grotzinger, J. P. Facies and evolution of Precambrian depositional systems: emergence of the modern platform archetype. *SEPM Spec. Publ.* **44**, 79–106 (1989).
29. Berner, R. A. Modeling atmospheric O<sub>2</sub> over Phanerozoic time. *Geochim. Cosmochim. Acta* **65**, 685–694 (2001).
30. Schlesinger, W. H. *Biogeochemistry* (Academic, San Diego, 1997).

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## A new troodontid dinosaur from China with avian-like sleeping posture

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Discovering evidence of behaviour in fossilized vertebrates is rare. Even rarer is evidence of behaviour in non-avian dinosaurs that directly relates to stereotypical behaviour seen in extant birds (avians) and not previously predicted in non-avian dinosaurs<sup>1,2</sup>. Here we report the discovery of a new troodontid taxon from the Early Cretaceous Yixian Formation of western Liaoning, China. Numerous other three-dimensionally preserved vertebrate fossils have been recovered recently at this locality, including some specimens preserving behavioural information<sup>3</sup>. The new troodontid preserves several features that have been implicated in avialan origins. Notably, the specimen is preserved in the stereotypical sleeping or resting posture found in extant Aves<sup>4</sup>. Evidence of this behaviour outside of the crown group Aves further demonstrates that many bird features occurred early in dinosaurian evolution<sup>5,6</sup>.

Theropoda Marsh, 1881  
Maniraptora Gauthier, 1986  
Troodontidae Gilmore, 1924  
*Mei long* gen. et sp. nov.

**Etymology.** *Mei* from Chinese, meaning to sleep soundly; *long* from Chinese, meaning dragon.

**Holotype.** IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing) V12733, a nearly complete, fully articulated skeleton (Fig. 1).

**Locality and horizon.** Lujiatun, Shangyuan, Beipiao City, western Liaoning, China; lowest more fluvial, volcanoclastic beds of Yixian Formation, older than 128 and younger than 139 million years<sup>7</sup>.

**Diagnosis.** *Mei long* is distinguishable from all other troodontids on

the basis of extremely large nares extending posteriorly over one-half of the maxillary tooth row; closely packed middle maxillary teeth; maxillary tooth row extending posteriorly to the level of the preorbital bar; a robust, sub-'U'-shaped furcula; presence of a lateral process on distal tarsal IV; and the most proximal end of the pubic shaft is significantly compressed anteroposteriorly, and extends laterally just ventral to the articulation with the ilium.

*Mei long* is about 53 cm in length, similar in size to the basal dromaeosaurid *Microraptor zhaoianus* and the basal avialan *Archaeopteryx lithographica*<sup>5,8,9</sup>. IVPP V12733 is not an adult, as several cranial sutures are unfused, and although fused, sutures between the neural arches and centra are still apparent on the dorsal vertebrae. However, the holotype is also not a hatchling as caudal and sacral vertebral sutures are not apparent, the parietal is formed from a single element and there is complete fusion of astragalus and calcaneum, indicating that the individual is approaching maturity.

As in *Sinovenator changii* and basal dromaeosaurs<sup>5</sup>, the skull is proportionally small (about 69% of the femoral length), the trunk short and the hindlimbs very long. Long hindlimbs relative to the trunk is a feature correlated with a knee-based avian running mechanism<sup>10</sup>; it is also present in the basal troodontids *Sinovenator* and *Sinornithoides*<sup>11,12</sup>, the basal dromaeosaurid *Microraptor*, and the basal oviraptorosaurian *Caudipteryx*<sup>5,10</sup>. As in other troodontids<sup>13,14</sup> the numerous maxillary teeth (approximately 24) are tightly packed anteriorly (Fig. 2a, b). Unlike other troodontids, even the middle teeth lack inter-crown space. Posteriorly, the teeth are more stout and re-curved. As with other troodontids<sup>5</sup>, the internarial bar is strap-like and 'T'-shaped. Additionally, a pneumatopore lies on the posterior quadrate surface; a prominent convexity lies lateral to the foramen magnum on the exoccipital/opisthotic; and the distally expanded pendulous paroccipital processes are vertical and apneumatic. The dentary nutrient foramina lie in a horizontal groove on the labial surface of the dentary as in other troodontids<sup>13,15</sup>.

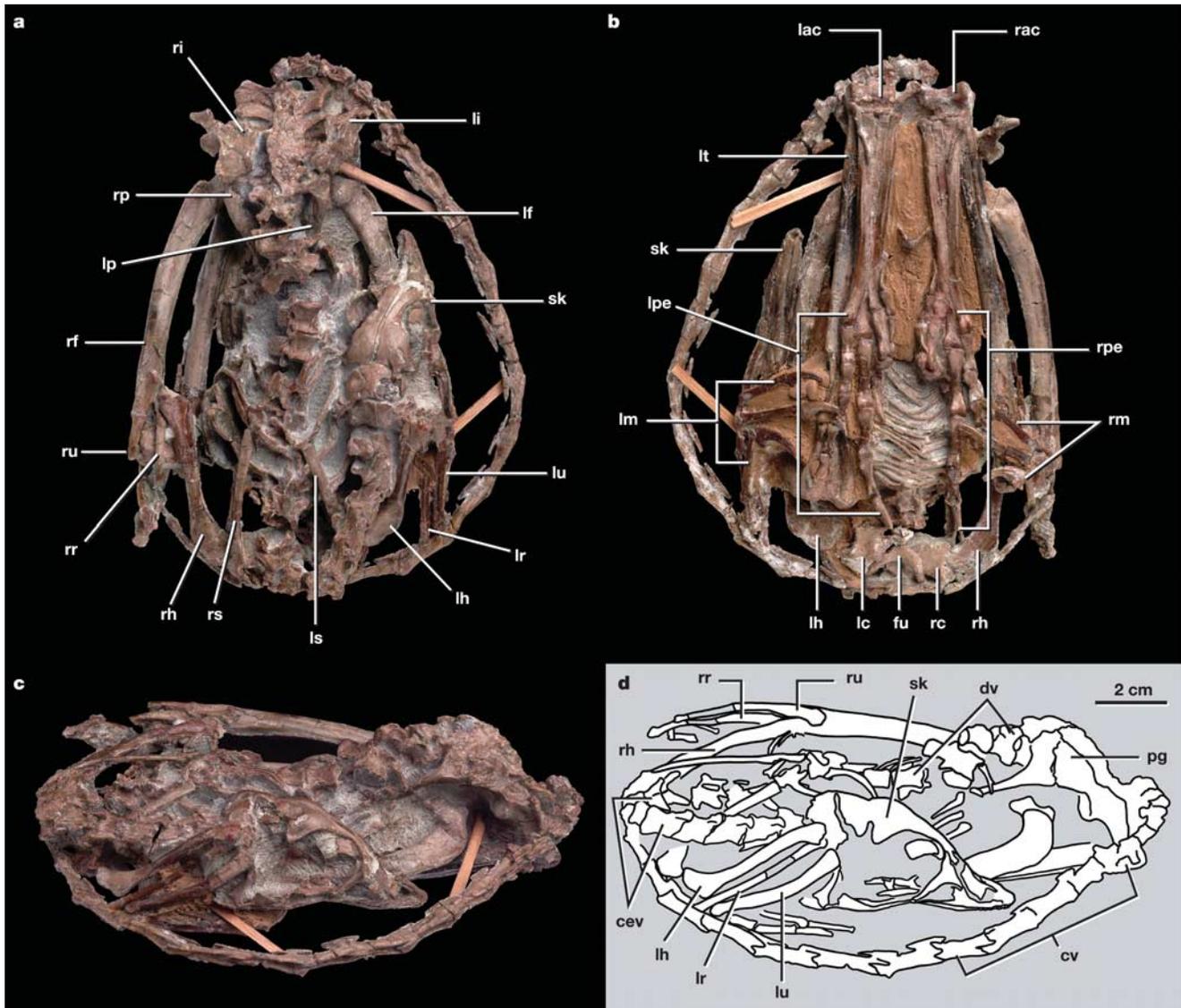
As in *Sinovenator changii* the dorsal vertebrae have fan-shaped neural spines and slender transverse processes, but lack pneumatic foramina<sup>6</sup>. The distal caudals are elongate, with a reduced centrum and a sulcus on their dorsal surface as in other troodontids<sup>12</sup>. The ilium is short and tapers posteriorly. The pubis is long and proximally thick, but is not mediolaterally compressed as in other troodontids including *Sinovenator changii*. The ischium is fairly short with a distally positioned obturator process and two small processes on the dorsal edge. The tibia has an anteroposteriorly wide proximal end, and a distal end with a thick lateral margin. As in basal dromaeosaurids and *Sinovenator*<sup>16,17</sup> the feet are subarctometatarsalian, and metatarsal III is reduced but still visible on the plantar surface (Fig. 1b). Metatarsal II bears a prominent medial flange and metatarsal IV a lateral one on the ventral surface, producing a longitudinal metatarsal palmar excavation. As in other deinonychosaurs, the second pedal digit is specialized with a hypertrophied claw, but is not developed to the same degree as seen in derived dromaeosaurids<sup>5,18</sup>.

*Mei long* differs with respect to a number of features compared with most other troodontids. Many of these differences are similar to conditions seen in avialans and dromaeosaurids<sup>5,17–19</sup>. Laterally, the skull has an antorbital fossa that is much smaller than that of other non-avian theropods (except for oviraptorosaurians<sup>5</sup>) and a large orbit that is apparently confluent with the infra-temporal fenestra (Fig. 2a, b). No postorbital is preserved, but if present it was undoubtedly small, as in *Archaeopteryx*<sup>9</sup>. As in avialans<sup>19</sup> and mononykines<sup>20</sup>, there is no corresponding ascending postorbital process of the thin jugal to form a complete postorbital bar; however, there is a small dorsal expansion of the jugal at its posterior end (as in *Archaeopteryx*<sup>19</sup>), near where it contacts the quadrate, which is buttressed by an extremely small quadratojugal (Fig. 2a, b). The squamosal is also reduced and does not contact the quadrato-

jugal, and the quadrate has a sharp and ventrally located pterygoid ramus. The snout is very short (Fig. 2a, b). The premaxilla has a large pre-naris portion and a long ascending process that accounts for about one-half of the snout length. The anterior projection of the maxilla is very long, and shallow, and forms the entire ventral border of the extremely large external nares that extend posteriorly over one-half of the length of the maxillary tooth row. Consequently, the nasals are short and consistently wide along their entire length. Comparatively, the frontal is elongate, about 45% the total length of the skull, and is blunt with a slight transverse expansion anteriorly. A sagittal crest is absent on the parietal. The braincase is expanded dorsoventrally and transversely (much wider than the minimum interorbital region). The supraoccipital crest is prominent, divided by an unclosed suture, and is hourglass-shaped, bordering distinct epiotic/opisthotic ossifications. The teeth are unserrated and distally re-curved as in *Byronosaurus*<sup>14</sup>. As in dromaeosaurids, the posterior dorsal vertebrae bear distinct para-

pophyses; however, they are not as stalk-like as those in advanced dromaeosaurs (for example, *Velociraptor*). The radius is thin and proportionally much longer than in other troodontids (see Supplementary Information), about 95% of the humeral length. A prominent proximally projected process lies on the lateral margin of distal tarsal IV, a feature otherwise only seen *Microraptor gui*. As in dromaeosaurids<sup>18</sup>, pedal phalanges II-1 and II-2 both have a medially centred ventral heel.

The holotype preserves and clarifies several unknown features of troodontids. The cervicals are incipiently heterocoelous as in some dromaeosaurids. The first and second dorsals bear prominent ventral processes on the anterior half of the centra, which are distally ball-like. Two small fragments of flat bones may represent sternal rib fragments as found in other maniraptorans<sup>18,21</sup>. A large furcula is present in loose articulation with the acromion process of the scapula. It is robust and flat in cross section, with an incipient hypocleidium and expanded distal articular ends (Fig. 2c), and is



**Figure 1** Holotype of *Mei long* (IVPP V12733). **a–c**, Photographs of the skeleton in dorsal (**a**), ventral (**b**) and dorsolateral (**c**) views. **d**, Line drawing of the skeleton in dorsolateral view. cev, cervical vertebrae; cv, caudal vertebrae; dv, dorsal vertebrae; fu, furcula; lac, left astragalus–calcaneum; lc, left coracoid; lf, left femur; lh, left humerus; li, left ilium; lm, left manus; lp, left pubis; lpe, left pes; lr, left radius; ls, left

scapula; lt, left tibia; lu, left ulna; pg, pelvic girdle; rac, right astragalus–calcaneum; rc, right coracoid; rf, right femur; rh, right humerus; ri, right ilium; rm, right manus; rp, right pubis; rpe, right pes; rr, right radius; rs, right scapula; ru, right ulna; sk, skull. Scale bar, 2 cm.

more 'U'-shaped and robust as in avialans rather than in dromaeosaurids<sup>5,17</sup>. As in dromaeosaurids and avialans, the scapulocoracoid is 'L'-shaped and the scapula is positioned close to the neural spines of the dorsals and is almost parallel to the vertebral column. The coracoid has a large coracoid tubercle, a sub-glenoid fossa and is divided into an anterodorsal and an anteroventral surface by a low

ridge, as in many other maniraptorans<sup>5</sup>. The humerus projects laterally and the forearm and the manus fold in an avian mode (Fig. 1a, b), as in other maniraptorans<sup>5</sup>.

Inclusion of *M. long* into a recent phylogenetic analysis<sup>22</sup> places *M. long* as the sister group to *Sinovenator* at the base of troodontids, and supports a monophyletic Deinonychosauria, which in turn is the sister group to Avialae (see Supplementary Information). For the included taxa this consensus solution is identical to that proposed by ref. 22.

Several studies have suggested that small size is crucial to the origin of flight and that miniaturization was responsible for many of the unique morphologies seen in avialans<sup>6,16,17</sup>; thus, *M. long* provides further evidence for this theory. For instance, *M. long* and *Archaeopteryx* lack a jugal–postorbital and a quadratojugal–squamosal contact<sup>9,19</sup>, and so might basal dromaeosaurids<sup>5,19</sup>. The nasal–frontal articulation is weak in *M. long* and possibly also in basal dromaeosaurs. These features suggest that some kind of cranial kinesis (probably prokinesis) evolved in the early evolution of eumaniraptorans. Notably, these features are also found in mononykines<sup>20</sup>. Derived larger members of the two deinonychosaurian groups often have the primitive states of these characters<sup>5,23</sup> and show a non-avian akinetic skull.

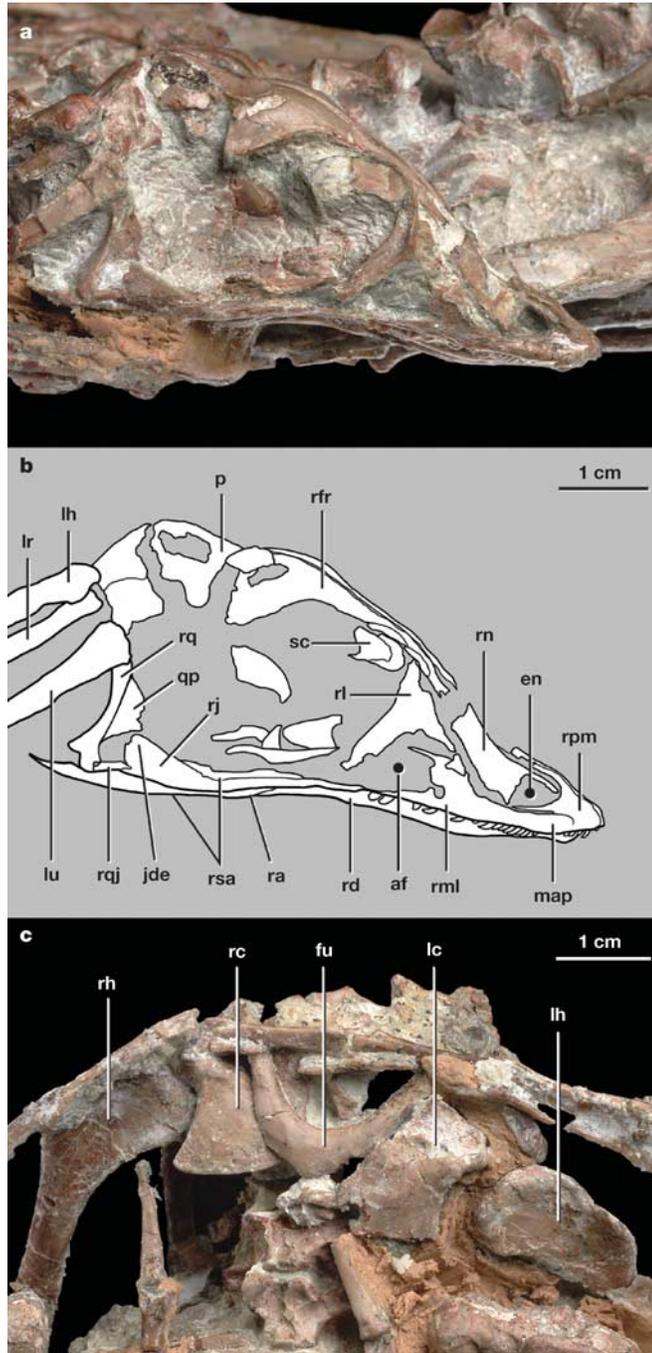
This specimen displays the earliest recorded occurrence of the stereotypical sleeping or resting behaviour found in living birds. The body sits on folded symmetrical hindlimbs. The forelimbs are also symmetrical and extend laterally, folded avian-like next to the body, with the elbows slightly displaced laterally relative to the trunk (the left elbow more than the right, with the distal-most manus underneath the knees). The neck curves posteriorly on the left side of the body so that part of the head lies medial to the left elbow at the side of the trunk. This posture is identical to the stereotypical 'tuck-in' sleeping posture of many living birds. In the *M. long* holotype, we propose that this posture represents a life posture for the animal captured when it was sleeping or resting on the ground, based on the sedimentary context and comparative pose data of most other dinosaur specimens (see Methods).

Living tetrapods display diverse sleeping and resting postures, but only avians and some mammals rest on their folded limbs. Avians, owing to their long and very flexible necks, differ from mammals in tucking their heads between one of their anterior appendages and their torso. The *M. long* holotype is preserved in a remarkable life pose, capturing this tuck-in sleeping (or resting) posture. In birds, the tuck-in posture reduces surface area and conserves heat in the head, a major region of heat loss in these animals<sup>24,25</sup>. It is therefore usually associated with heat conservation<sup>24,25</sup>. From the phylogenetic position of the fossil we can tell that the tuck-in behaviour originated in the non-avian precursors to modern birds. Although we are unable to measure it directly, the physiological/thermal implications of this and other fossil evidence (for example, brooding and feathers) are highly suggestive that these animals shared a homeothermic physiology with modern avians. □

Methods

Life posture inference

The holotype of *M. long* is inferred to be buried in deposits when the animal was sleeping or resting, and thus preserves a life posture. Exceptionally well-preserved vertebrate specimens have been collected from the Lujiatun beds over the last few years, and it has been proposed that some of them provide information for dinosaur behaviour<sup>3</sup>. The Lujiatun beds are alluvial deposits mainly comprising tuffaceous conglomerate debris flows, sandstones and mudstones<sup>26</sup>. Some of the most fossiliferous locations are considered to be the result of instant catastrophic mass mortality events<sup>26,27</sup> preserved in tuffaceous ashes up to 3 m in thickness. Although not all are volcanic in origin, such Pompeii-like depositional conditions are present in other localities that preserve behavioural characters in fossil vertebrates<sup>1,28</sup>. Other dinosaur specimens from the lacustrine beds of the Yixian formation<sup>26</sup> and specimens from the more classically fluvial lower sandstone beds (such as *Shenzhousaurus*<sup>29</sup>) are not preserved in life posture, but in more typical death poses with heads bent back above the spine and the hind appendages and tails extended<sup>30</sup>. Both the specimen itself and the sedimentology of the deposits from which this specimen was collected indicate that the preserved posture represents a life posture for the animal. Such a



**Figure 2** Holotype of *Mei long* (IVPP V12733). **a, b**, Photograph (**a**) and line drawing (**b**) of skull in right lateral view. Note that the right external naris is much smaller than its actual size due to the anterior displacement of the right nasal. **c**, Furcula in anterior ventral view. af, antorbital fossa; en, external naris; jde, dorsal extension of posterior jugal; map, anterior projection of the maxilla; p, parietal; qp, pterygoid process of quadrate; ra, right angular; rd, right dentary; rfr, right frontal; rj, right jugal; rl, right lacrimal; rml, right maxilla; rn, right nasal; rpm, right premaxilla; rq, right quadrate; rqj, right quadratojugal; rsa, right surangular; sc, sclerotic plates. Scale bar, 1 cm.

posture can also be inferred from the Early Cretaceous troodontid *Sinornithoides* from the Ordos basin and perhaps for the nesting oviraptorid *Citipati* (IGM 100/979); however, these specimens are incomplete and more distorted<sup>11</sup>.

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1. Norell, M. A., Clark, J. M., Chiappe, L. M. & Dashzeveg, D. A nesting dinosaur. *Nature* **378**, 774–776 (1995).
2. Varricchio, D. J., Jackson, F., Borkowski, J. J. & Horner, J. R. Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. *Nature* **385**, 247–250 (1997).
3. Meng, Q.-J., Liu, J. Y., Varricchio, D. J., Huang, T. & Gao, C.-L. Parental care in an ornithischian dinosaur. *Nature* **431**, 145–146 (2004).
4. Wing, L. W. *Natural History of Birds* (Ronald Press, New York, 1956).
5. Xu, X. *Deinonychosaurian fossils from the Jehol Group of western Liaoning and the coelurosaurian evolution*. PhD dissertation, Chinese Academy of Sciences (2002).
6. Sereno, P. C. The evolution of dinosaurs. *Science* **284**, 2137–2147 (1999).
7. Swisher, C. C. III *et al.* Further support for a Cretaceous age for the feathered-dinosaur beds of Liaoning, China: New <sup>40</sup>Ar/<sup>39</sup>Ar dating of the Yixian and Tuchengzi Formations. *Chin. Sci. Bull.* **47**, 135–138 (2002).
8. Xu, X., Zhou, Z. H. & Wang, X. L. The smallest known non-avian theropod dinosaur. *Nature* **408**, 705–708 (2000).
9. Elzanowski, A. in *Mesozoic Birds: Above the Heads of Dinosaurs* (eds Chiappe, L. M. & Witmer, L. M.) 129–159 (Univ. California Press, Berkeley, 2002).
10. Jones, T. D., Farlow, J. O., Ruben, J. A., Henderson, D. M. & Hillenius, W. J. Cursoriality in bipedal archosaurs. *Nature* **406**, 716–718 (2000).
11. Russell, D. A. & Dong, Z.-M. A nearly complete skeleton of a new troodontid dinosaur from the Early Cretaceous of the Ordos Basin, Inner Mongolia, People's Republic of China. *Can. J. Earth Sci.* **30**, 2163–2173 (1994).
12. Currie, P. J. & Dong, Z. New information on Cretaceous troodontids (Dinosauria, Theropoda) from the People's Republic of China. *Can. J. Earth Sci.* **38**, 1753–1766 (2001).
13. Currie, P. J. Bird-like characteristics of the jaws and teeth of troodontid theropods (Dinosauria: Saurischia). *J. Vert. Paleontol.* **7**, 72–81 (1987).
14. Norell, M. A., Makovicky, P. J. & Clark, J. M. A new troodontid theropod from Ukhaa Tolgod, Mongolia. *J. Vert. Paleontol.* **20**, 7–11 (2001).
15. Makovicky, P. J., Norell, M. A., Clark, J. M. & Rowe, T. Osteology and relationships of *Byronosaurus jaffei* (Theropoda: Troodontidae). *Am. Mus. Novit.* **3402**, 1–32 (2003).
16. Xu, X., Norell, M. A., Wang, X. L., Makovicky, P. J. & Wu, X. C. A basal troodontid from the Early Cretaceous of China. *Nature* **415**, 780–784 (2002).
17. Hwang, S. H., Norell, M. A., Ji, Q. & Gao, K.-Q. New specimens of *Microraptor zhaoianus* (Theropoda: Dromaeosauridae) from northeastern China. *Am. Mus. Novit.* **3381**, 1–44 (2002).
18. Norell, M. & Makovicky, P. J. Important features of the dromaeosaur skeleton: information from a new specimen. *Am. Mus. Novit.* **3215**, 1–28 (1997).
19. Chiappe, L. M., Ji, S.-A., Ji, Q. & Norell, M. A. Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the late Mesozoic of Northeastern China. *Bull. Am. Mus.* **242**, 1–89 (1999).
20. Chiappe, L. M., Norell, M. A. & Clark, J. M. The skull of a relative of the stem-group bird *Mononykus*. *Nature* **392**, 275–282 (1998).
21. Clark, J. M., Norell, M. A. & Chiappe, L. M. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianlike brooding position over an oviraptorid nest. *Am. Mus. Novit.* **3265**, 1–35 (1999).
22. Hwang, S. H., Norell, M. A., Ji, Q. & Gao, K.-Q. A large compsognathid from the Early Cretaceous Yixian Formation of China. *J. Syst. Palaeontol.* **2**, 13–30 (2004).
23. Barsbold, R. & Osmolska, H. The skull of *Velociraptor* (Theropoda) from the Late Cretaceous of Mongolia. *Acta Palaeontol. Polonica* **44**, 189–219 (1999).
24. Hill, R. W., Beaver, D. L. & Veghte, J. H. Body surface temperatures and thermoregulation in the black-capped chickadee (*Parus atricapillus*). *Physiol. Zool.* **53**, 305–321 (1980).
25. Marsh, R. L. & Dawson, W. R. Avian adjustments to cold. *Adv. Comp. Environ. Physiol.* **4**, 205–253 (1989).
26. Chang, M.-M., Chen, P.-J., Wang, Y.-Q., Wang, Y. & Miao, D.-S. *The Jehol Biota* (Shanghai Scientific & Technical Publishers, Shanghai, 2003).
27. Guo, Z., Liu, J. & Wang, X. Effect of Mesozoic volcanic eruptions in the western Liaoning Province, China on paleoclimate and paleoenvironment. *Sci. Chin. Ser. D* **46**, 1261–1272 (2003).
28. Loop, D. B., Dingus, L., Swisher, C. C. III & Minjin, C. Life and death in a Late Cretaceous dune field, Nemegt basin, Mongolia. *Geology* **26**, 27–30 (1998).
29. Ji, Q. *et al.* An early ostrich dinosaur and implications for ornithomimosaur phylogeny. *Am. Mus. Novit.* **3420**, 1–19 (2003).
30. Schweitzer, M. H. & Marshall, C. L. A molecular model for the evolution of endothermy in the theropod-bird lineage. *J. Exp. Zool.* **291**, 317–338 (2001).

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## Adaptation varies through space and time in a coevolving host–parasitoid interaction

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One of the central challenges of evolutionary biology is to understand how coevolution organizes biodiversity over complex geographic landscapes. Most species are collections of genetically differentiated populations, and these populations have the potential to become adapted to their local environments in different ways. The geographic mosaic theory of coevolution incorporates this idea by proposing that spatial variation in natural selection and gene flow across a landscape can shape local coevolutionary dynamics<sup>1–7</sup>. These effects may be particularly strong when populations differ across productivity gradients, where gene flow will often be asymmetric among populations<sup>8</sup>. Conclusive empirical tests of this theory have been particularly difficult to perform because they require knowledge of patterns of gene flow, historical population relationships and local selection pressures<sup>2</sup>. We have tested these predictions empirically using a model community of bacteria and bacteriophage (viral parasitoids of bacteria). We show that gene flow across a spatially structured landscape alters coevolution of parasitoids and their hosts and that the resulting patterns of adaptation can fluctuate in both space and time.

Bacteria and bacteriophage have been used as model organisms for ecological and evolutionary studies since at least the 1960s and have proven particularly useful for studies of antagonistic coevolution<sup>9–13</sup>. The coevolutionary dynamics of the bacterium *Escherichia coli* and the bacteriophage T7 are well studied, and can be divided into a series of phenotypic classes based on patterns of resistance and counter-resistance<sup>9</sup>. Ancestral, T7-sensitive bacteria (B<sub>0</sub>) evolve resistance to ancestral bacteriophage (T7<sub>0</sub>), after which they are referred to as first order resistant bacteria (B<sub>1</sub>). This change most often occurs through mutations that change or eliminate the cell surface receptor molecule. T7 can then evolve to attack the first order resistant bacteria and are referred to as host-range mutants (T7<sub>1</sub>). Most often this occurs through mutations that change the T7 tail fibres, resulting in an expanded host range (that is, T7<sub>1</sub> are able to attack both B<sub>0</sub> and B<sub>1</sub>). Second order resistant bacteria (B<sub>2</sub>) that are resistant to T7<sub>0</sub> and T7<sub>1</sub> can also arise and eventually invade the community. T7 have not yet been observed to evolve the ability to infect B<sub>2</sub> (ref. 9). Because T7 directly kills the bacteria that it infects and also the generation time of T7 is shorter than that of its host, T7 can be thought of as a parasitoid rather than a parasite or predator.

We evaluated how dispersal across a spatially structured landscape shapes the coevolutionary dynamics of *E. coli* and T7 by establishing a stepping-stone, source–sink experimental landscape of microbial communities. We directly manipulated dispersal of T7 and *E. coli* along a resource (productivity) gradient in two landscapes (Fig. 1). In one landscape, continuous culture devices (chemostats) containing T7 and *E. coli* were linked by dispersal in a stepping-stone fashion. Every two days, we dispersed 10% of the community from the highly productive source community to a community with an intermediate level of resources, and then 10% of that community to a low productivity (sink) community. In the